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Trophic interactions in centipedes (Chilopoda, Myriapoda) as indicated by fatty acid patterns: Variations with life stage, forest age and season

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ABSTRACT

Fatty acid (FA) analysis investigates changes in the relative contribution of prey from major energy channels in decomposer food webs for predator nutrition. Adopting this approach we investigated whether the trophic niche of centipedes, as major invertebrate predators in forest soil food webs, changes with maturation, season or forest age. Generally, each of the four centipede species studied differed significantly in their FA composition suggesting trophic niche differentiation. FA profiles differed more strongly in the two geophilomorph (*Strigamia acuminata* and *Geophilus ribauti*) than in the two lithobiomorph species (*Lithobius crassipes* and *Lithobius mutabilis*) suggesting that in particular the former feed on markedly different prey. FA profiles changed during post-embryonic development in each of the four centipede species. Differences were most pronounced in the two lithobiomorph species shifting to predominantly fungal feeding prey. Further, FA profiles varied with season indicating that centipedes exploit more prey out of the bacterial channel in autumn. FA profiles of centipedes varied little with forest age suggesting that soil food webs are remarkably invariant across different forest ecosystems. The results indicate that FA composition of second order consumers closely reflects changes in diet of prey species and composition of basal resources. The study proved FA profiles as powerful tool to gain insight into critical characteristics of soil food web stability, i.e., compartmentalisation and the relative importance and variability of energy channels.

1. Introduction

Trophic interactions in soils are still largely unexplored as they are complex and difficult to disentangle (Scheu and Setälä, 2002). In soil food webs fungi and bacteria represent the major components of microbial biomass comprising basal prey for many consumers. Their ratio varies with organic matter content and other factors, such as pH and soil texture (Salamon et al., 2008; Fierer et al., 2009). In comparison to fungi, bacteria are more sensitive to desiccation (Bardgett, 2005; Gordon et al., 2008). Kilbertus et al. (1982) found the bacterial densities to be highest in June and July due to high soil moisture and lowest in November and December due to frost in deciduous forests. Microbial communities in old-growth forests are dominated by fungi (Bauhus et al., 1998; Pennanen et al., 1999; Moore-Kucera and Dick, 2008). These variations are likely to propagate into higher trophic levels, such as microbivores but also to top-predators.

A novel approach for investigating soil food webs is the analysis of fatty acids (FAs) where FAs can be traced from one trophic level to another, uncovering the diet of consumers and consequently food web links (Ruess et al., 2002; Ruess and Chamberlain, 2010). In consumers, most of the assimilated FAs are converted into neutral lipid FAs (NLFAs) in the fat body which may comprise a large fraction of their body mass. Since it is energetically more efficient to incorporate FAs without modification ("dietary routing"; Blem, 1976; Pond, 1981), NLFAs of the fat body reflect the FA composition of the food sources to a significant extent (Ruess et al., 2004) and therefore, allow tracing feeding strategies. Haubert et al. (2006) showed that variations in the composition of NLFAs in Collembola due to dietary changes are more pronounced than variations between collembolan species.

Some FAs can serve as absolute biomarkers, as their synthesis is specific for certain organism groups; e.g., the only organisms in soil able to synthesise methyl-branched (iso, anteiso) and cyclic FAs are bacteria (Zelles, 1997, 1999) and therefore, if present in consumers, these FAs reflect bacterial prey (Ruess et al., 2005; Ruess and Chamberlain, 2010). On the other hand, there are FAs which are present in different organisms but predominate in certain taxa; e.g., linoleic acid (18:2ω2,6) predominantly occurs in fungi and is enriched in fungal feeders thereby functioning as relative marker. Plants synthesise both linoleic acid and oleic acid (18:1ω9), but the

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proportion of linoleic acid is considerably lower than in fungi. Therefore, oleic acid can be used as a relative marker for plants. Further, the ratio of both relative markers has been used to distinguish between plant and fungal feeding (Ruess et al., 2007; Ruess and Chamberlain, 2010). Vaccenic type FAs (16:1ω7, 18:1ω7) predominantly occur in bacteria and have been suggested as additional bacterial biomarkers (Ruess and Chamberlain, 2010). Long-chain polyunsaturated FAs (PUFAs) with 20 or more carbon atoms, such as 20:4ω6, 20:5ω3 and 20:2ω6, are widespread in animals (Chamberlain and Black, 2005) and algae (Dunstan et al., 1994), but lacking in fungi and most bacteria. FAs which are modified after consumption or to a large extent synthesised de novo are not suitable for tracing food relationships (Pollierer et al., 2010).

Recently, it has been documented for soil animal food webs that FAs can be traced over more than one trophic level allowing the investigation of trophic channels based on bacteria and fungi in soil (Ruess et al., 2004; Pollierer et al., 2010). In laboratory systems Pollierer et al. (2010) showed that bacterial, fungal and plant marker FAs ingested by Collembola were also incorporated by predators (centipedes and spiders) after feeding on these Collembola. This raises the opportunity to investigate trophic interactions of predatory soil macroarthropods in the field.

Following FAs of basal taxa through food webs, FA analysis combines advantages of other powerful tools for analysing food webs, i.e., stable isotope analysis and molecular gut content analysis (Tiunov 2007, King et al., 2008). Compared to molecular gut content analysis FA analysis integrates consumption of food sources over a longer period of time, whereas, compared to stable isotope analysis, changes in diet become apparent more quickly, making this method suitable for the investigation of intermediate time intervals, such as different seasons or developmental stages. Haubert et al. (2011) tested the retention time of FAs in Collembola and found FAs of food sources to be already present in consumer tissue after one day and still being detectable after 14 days. Once incorporated the half-life of fatty acid carbon in consumers is short, e.g., 1.5–5.8 days in Collembola (Chamberlain et al., 2004), allowing to trace changes of feeding strategies with life stage and season. However, interpretation of results has to account for physiological and environmental factors influencing FA composition of consumers. During starvation the concentrations of FAs change indiscriminately between FAs, with the FA composition remaining constant (Haubert et al., 2004). Further, Haubert et al. (2004) found that changes in food quality affected FA compositions of Collembola only slightly. In winter the amounts of unsaturated FAs increase which is well known for PLFAs in membranes but may be even stronger for NLFAs (Haubert et al., 2008; Jagdale and Gordon, 1997; Petersen and Holmstrup, 2000; van Dooremalen and Ellers, 2010). However, Holmstrup et al. (2002) found that NLFA composition changed only little with acclimation to low temperatures.

Centipedes are the dominant invertebrate predators in soil in European beech forests (Poser, 1990; Scheu and Falca, 2000). The two centipede subgroups prevailing in Central Europe are Lithobiomorpha and Geophilomorpha which differ in life history, development, nutrition and the microhabitats they colonise. Lithobiomorpha are sit-and-wait predators in the litter layer whereas Geophilomorpha predominantly search for prey in mineral soil (Wolters and Ekschmitt, 1997). A marked exception of the latter is *Strigamia acuminata* (Leach) which predominantly hunts in the litter layer (Poser, 1990). Poser (1990) provided evidence supporting earlier assumptions that Lithobiomorpha feed on small mobile prey, whereas Geophilomorpha feed on large and little mobile prey. Gut contents of Lithobiomorpha comprised great amounts of mite and collembolan proteins, whereas gut contents of Geophilomorpha were dominated by lumbricid and enchytraeid proteins. Recent molecular gut content analyses of centipedes confirmed these findings, but also detected collembolan prey in Geophilomorpha (B. Eitzinger, unpublished results). However, whether these patterns are valid for different species and also apply for juveniles remains unknown. Further, little is known on the feeding behaviour of soil predators in winter (Aitchison, 1984a, 1984b, 1986; Eitzinger and Traugott, 2011).

This study aims at analysing trophic niches of centipedes and to trace their links to bacterial and fungal energy channels in the soil food web of deciduous forests using FA analysis. To allow comprehensive insight into trophic relationships we analysed if trophic niches varied with life stage, season and forest age. We hypothesised that the two centipede groups, Lithobiomorpha and Geophilomorpha, are associated with different energy channels i.e., the fungal and bacterial channel, as they differ in biological traits. Different life stages of centipedes are expected to differ in their association with energy channels due to shifts in prey spectra. Further, we hypothesised that the associations with the fungal energy channel are more pronounced in summer as fungi are less sensitive to drought, whereas wet conditions in autumn favour associations with the bacterial energy channel. Finally, we expected association of centipedes to the fungal energy channel to be more pronounced in old-growth forests than in younger forests.

2. Materials and methods

2.1. Study sites

The study was set-up in the Hainich, a mountain range in Thuringia in eastern Germany at an altitude of 330–490 m a.s.l. Sedimentary rock is formed by a Mesozoic cuesta landscape with limestone. The soil type is Stagnic and Haplic Luvisol with pH ranging from 4.0 to 4.8. Four different forest sites were investigated, two old-growth beech stands of an age of about 120 years and two young beech stands of an age of about 30 years. Generally, the forest in the Hainich is dominated by European beech (*Fagus sylvatica* L.) with ash (*Fraxinus excelsior* L.) and maple (*Acer pseudoplatanus* L.) being interspersed. The herb layer in the Hainich consists predominantly of spring geophytes, such as *Allium ursinum* (L.), *Anemone nemorosa* (L.) and *Galium odoratum* ((L.) Scopoli). In the 120 years old forest sites a sparse shrub layer of blackberry (*Rubus* spec. L.) was present. Climate at the Hainich is suboceanic with an annual average temperature of about 7 °C and a total annual precipitation of about 750 mm. Mean temperatures for the sampling months June and October 2009, and February 2010 were 14.2 °C, 7.7 °C and −1.2 °C, respectively (H. Coners, unpublished data).

2.2. Centipedes

Centipedes were sampled in three consecutive seasons i.e., in June (5th, 10th, 15th and 22nd) and late October (20th, 29th and 31st) 2009, and in February (1st, 8th and 28th) 2010. At each date within one season, temperature was similar. Litter was sieved through 18 mm mesh and centipedes of all size classes were collected, transferred individually into Eppendorf tubes and stored in a cooled box for transport. Additionally, litter was collected and animals were extracted by heat in the laboratory (Kempson et al., 1963). All animals were collected alive and frozen at −22 °C until identification and processing.

The two dominant lithobiomorph species [*Lithobius crassipes* (Koch) and *Lithobius mutabilis* (Koch)] and geophilomorph species [*S. acuminata* and *Geophilus ribauti* (Brölemann)] were selected for the analyses. In Lithobiomorpha the third larval stage, the first to second post-larval stage and adults were sampled. In Geophilomorpha two size classes representing juvenile and adult individuals were differentiated. In *S. acuminata* small individuals